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Intraherd prediction of beef cattle genetic values using linear model techniques

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INTRAHERD PREDICTION OF BEEF CATTLE GENETIC VALUES USING LINEAR MODEL TECHNIQUES

Iowa State University PH.D. 1983

Intraherd prediction of beef cattle genetic values using linear model techniques

by

Brett Keith Middleton

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Population structures in the livestock industry have always been responsive to technological advance. In recent decades, the existence of artificial insemination and improvements in transportation and communication have increased the movement of germ plasm between herds; the replacement pool available to the seedstock breeder has gone from neighborhood size, as described by Lush (1945), to national, continental, and even global size. Beef breeds are becoming analogs of single herds in earlier times (Willham, 1979), within which herds have become comparable to family lines (McGilliard, 1952).

This change in the population structure has prompted many to call for improved evaluation programs (e.g., Chapman et al., 1972; Pollak et al., 1977; Willham and Leighton, 1978; Willham, 1979; Warwick, 1980) that provide both breedwide genetic rankings for young animals and within-herd estimates of genetic and environmental trends. Defects in current industry programs prevent them from satisfying the informational requirements of beef breeders practicing interherd selection on the modern scale.

In the design of beef, as opposed to dairy, improvement programs, consideration must be given to the ability to measure traits of interest on animals of both sexes at an early age. Warwick (1980) discusses the change in beef programs from pedigree and progeny evaluations to performance testing during the 1940s, 50s, and 60s, noting that performance testing has always been stressed as being a within-herd selection tool. The common estimates of breeding value are not validly compared across

herds and do not account for the effects of competition or genetic trend. The initial industry response to the need for across-herd selection tools was the national sire evaluation (NSE), which uses mixed-model analysis of progeny records to produce best linear unbiased predictors (BLUP) of sire genetic merit.

The dairy industry has generally lead the beef industry in the development of evaluation methods, mostly because of the quantity of field data available to researchers since the formation of the first dairy herd improvement association in 1905 (Freeman, 1980). The NSE methods currently in use are no exception; Henderson (1966) presented the seminal paper outlining the use of BLUP techniques for dairy sire evaluation. Thus, NSE was developed in a dairy context; current beef programs have sacrificed the advantage of performance testing in favor of the progeny test. As Willham (1979) states:

> To let the beef industry become married to the progeny test as the only way to estimate the breeding value of sires would be tragic, since only performance and relative information can be used effectively to minimize the generation interval.

Therefore, the next phase of beef evaluation programs must be to combine the superiority of BLUP methodology with the leverage of early performance information. Intraherd BLUP would complement NSE programs by providing the best possible evaluation of females and young stock as well as the extra benefit of intraherd genetic and environmental trend estimates. The importance of the latter benefit is clearly shown by Brumby (1961), Harville and Henderson (1967), and McMaster (1982).

This conception of intraherd evaluation still fails, though, to grant a reasonable degree of confidence in making interherd selection

decisions. McGilliard (1952) envisioned interherd selection as a two-step process akin to combined family and individual selection: selection of a superior herd from which to select superior individuals. Instead, the unification of herd and individual information should be possible with current evaluation techniques. Still, neither tactic can be investigated without some means of quantifying herd genetic differences. Warwick (1980) claims,

> Insufficient ties between herds have been available to permit extrapolation of individual and family records to a breedwide basis and thus evaluate [animals] relative to probable standing within their breed;

however, this view is contradicted by the existence of accurate, large-scale, field-data sire evaluations as reported by Berger and Willham (1980) and Berger et al. (1982a, b, c, 1983). The computers, algorithms, and data are available to make what Willham and Leighton (1978) call "the logical extension" of intraherd BLUP: the use of NSE results to tie intraherd predictors to a common base for interherd comparisons.

This dissertation algebraically derives an adjustment factor for herd genetic merit from national sire evaluation procedures and discusses its use in intraherd evaluation. The behavior of this adjustment is then explored via simulated records. Treatment is given both the general suitability of the adjustment and the relationships between the error of adjustment and measures of the strength of the ties between herds.

REVIEW OF LITERATURE

Intraherd Evaluation

Comparisons within herd

Methods making use of progeny averages, deviations from subclass averages, and ratios were among the first to attempt more accurate representation of genetic merit by removal of environmental effects. Perhaps the worst failing of these methods was the assumption that there was no sampling error associated with the available records; differing numbers of records per animal or progeny per sire were not taken into account (Richey, 1971; Pollak et al., 1977). Those index techniques which Henderson (1974) classes as best prediction (BP) or best linear prediction (BLP) overcome this failing but are biased by other factors, such as genetic trend (Hillers, 1965), preferential (assortative) mating (Hillers, 1965), and sequential culling (Emsley et al., 1972). In general, BP and BLP methods don't rank animals well across contemporary groups and should be replaced for intraherd evaluation with the more advanced method of best linear unbiased prediction (BLUP) according to Pollak et al. (1977).

As Henderson (1966) provided the seminal description of BLUP sire evaluation techniques, so Henderson (1975b) has provided the seminal description of intraherd BLUP. A number of workers (e.g., Boyle et al., 1983; Schaeffer, 1983) have studied the use of Henderson's (1975b) model for dairy cow evaluation, and this method is now in regular use for evaluating cows in dairy herd improvement association herds in the northeastern United States (Bolgiano et al., 1980).

The most extensive treatment of the basic intraherd model and its permutations in the context of beef cattle evaluation is given by Quaas and Pollak (1980). This basic model is usually referred to as the genotypic or animal model and differs from the sire evaluation model in that each equation contains a term for the genetic value of the individual which made the record. More specifically,

$$y = X\beta + Zu + e,$$

where y = the vector of records,

β = the vector of fixed effects related to records by known incidence matrix X,

u = the vector of random breeding values related to records by known incidence matrix Z, and

e = the vector of random errors associated with each observation.

The concomitant assumptions are that

$$E[u] = E[e] = \phi, \text{ and}$$

$$V\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_u^2 & \phi \\ \phi & \sigma_e^2 \end{bmatrix},$$

where A is the numerator relationship matrix for all animals to be evaluated. The solutions to equations under this model will properly account for competition, genetic trend, preferential mating, and, in the multiple trait case, sequential culling. In addition, estimates of genetic and environmental trends can easily be obtained using this model. One important use of these is given by Harville and Henderson

(1967), who state that failing to account for trends can bias the computation of age-of-dam correction factors.

The multiple-trait intraherd models developed by Quaas and Pollak (1980) are studied by Pollak and Quaas (1981) via simulated beef records. These models include both direct and maternal weaning weight, maternal permanent environment, and postweaning gain. While Quaas and Pollak (1980) believe that the full multiple-trait animal model can be handled by modern computing facilities, they call the resulting equations "formidable" and devote considerable effort to developing reduced versions by applying the concept of equivalent models, defined as those which generate the same first and second moments of the observations. One justification for these efforts is the finding of Pollak and Quaas (1981) that the unreduced equations behave poorly when using an iterative solution technique.

The papers of Slanger (1979) and Slanger (1980) examine the reduction of the multiple-component weaning-weight model equations through simply omitting the equations for which solutions are not desired. Slanger (1979) develops this approach, and Slanger (1980) tests it on a set of Angus weaning weight records by solving three sets of equations: the full set and two reduced sets. Slanger (1980) found high correlations, few rank changes, and small absolute differences among the three solution vectors. Quaas and Pollak (1980), however, disagree with this approach to reducing the equations because it is not exact, unlike the equivalent-models approach.

In addition to doubts about the need and technique for reducing the intraherd equations, other questions concerning the structure of intra-

herd models, such as the need to account for inbreeding (Pollak and Ufford, 1978) and the need for genetic groups (Pollak et al., 1977; Famula and Van Vleck, 1982; Famula et al., 1983), remain unanswered.

Comparisons between herds

A number of researchers (e.g., Specht and McGilliard, 1960; Thompson, 1968; Alenda et al., 1982) have shown the practical importance of minimizing generation intervals to increasing rates of genetic progress. Even in dairy selection programs, Specht and McGilliard (1960) and Thompson (1968) demonstrate that progeny testing is often not the most advantageous procedure, though young bulls must frequently be selected on pedigree information alone.

National sire evaluation (NSE) programs in the beef industry are of little aid in selecting young sires because of the minimum accuracy limitation placed on the publication of expected progeny differences; Middleton and Berger (1983) reported the average age of published sires in the 1983 Polled Hereford Sire Summary as 12 years. Intraherd BLUP solves the problem of fairly evaluating young sires in relation to their parents but may be of little more use than the NSE because intraherd BLUP will not support the many important across-herd selection decisions if there are large genetic differences between herds. Willham and Leighton (1978), Willham (1979), and Quaas and Pollak (1980) all state that the extension of intraherd evaluation for interherd comparisons is vital if dependence on progeny testing is to be reduced.

Powell and Freeman (1974) and Spike and Freeman (1977) name two possible sources of genetic differences among herds. One source is

sampling differences; i.e., the average relationship among animals is greater within than across herds, and each herd contains a different sample from the population gene pool. If herds contained random samples, one would expect a uniform relationship within and between herds, though chance might still cause differences among such samples. The other source is genetic trend or selection pressures common to animals within herds.

There are several reports in the literature which deal with sampling effects. McDaniel and Corley (1967), working with milk production, and Bell et al. (1982), working with type score, each divided a number of dairy cows into several merit groups and found that groups had a strong influence on sire predicted differences (PD) calculated within group. McDaniel and Corley (1967) conclude that rankings within group were correct but that absolute breeding merit was not established. In each paper, the PD of sires within the groups of higher merit were biased downward. Emsley et al. (1972) conclude that computing ratios to a highly selected mean for beef cattle yearling weight could penalize superior animals by as much as 10% in comparisons with ratios in groups less heavily culled. Thus, the effect of sampling based on a single trait can be quite large. Differences between beef herds because of sampling under divergent selection goals can also be large, as shown by Chapman et al. (1972).

Whether or not initial sampling differences between herds exist, such differences can be created if intraherd genetic trends are not relatively homogeneous across the population. Arave et al. (1964) examined 11,993 fat-corrected milk records made by 3,900 cows in 12

California Jersey herds over 30 years. They estimated the overall genetic trend at 34 kg/yr or 0.7% of the mean per year. This agrees closely with the 0.5%/yr finding of Van Vleck and Henderson (1961) for the natural-service Holstein sire population in the northeast from 1951 to 1959. Even though this overall trend is modest, Arave et al. (1964) calculated intraherd trends ranging from -23 kg/yr to 66 kg/yr. There have not yet been any similar beef studies, but the overall trends for three major beef breeds are given in Table 1; the reader may draw his own conclusions about the possible variety of intraherd trends in these breeds. The trends in Table 1 are probably comparable, on a percentage basis, with the dairy trends cited above.

Table 1. Genetic trends for three beef breeds[a]

Breed	Years	Report	BWT[b]	WWT[c]	YWT[d]
Angus	1964-1979	Berger et al. (1982b)	0.03	0.49	1.16
Hereford	1964-1979	Berger et al. (1982c)	-0.04	0.88	1.66
Polled Hereford	1966-1980	Berger et al. (1983)	0.03	0.93	1.48

[a]All trends in kg/yr.

[b]Birth weight.

[c]Weaning weight.

[d]Yearling weight.

The sources of genetic herd differences have been established, but do these differences exist in actual field data? To partition herd differences into genetic and environmental components requires data in

which there are large paternal half-sib groups divided among two or more herds (Brumby, 1961; Cundiff et al., 1975). Dairy researchers have had records of this type since the early 1950s, but over two decades, more elapsed before the major beef breeds reduced their restrictions on the use of AI and made this kind of data available to beef researchers. Therefore, there has only been a single study of heritable herd differences in beef cattle (Cundiff et al., 1975), though the study of beef populations through field data should soon become a more important endeavor (Willham, 1982).

There are numerous references dealing with herd differences in dairy populations. Henderson et al. (1954) reports that 50% of the phenotypic variation for both milk and fat is due to herd differences; however, no attempt is made to determine the heritability of these. Brumby (1961), Morillo and Legates (1970), and Spike (1975) all state that up to 10% of the between-herd variation in milk and/or fat is genetic in nature. On the other hand, McGilliard (1952) states that 33% of the milk differences among Jersey Herd Improvement Registry herds are genetic, while Schaeffer et al. (1982) report genetic fractions of 2.05% and 12.74% for milk and fat, respectively, among Canadian Record of Performance herds.

A few workers have investigated the between-herds portion of the phenotypic variance of beef cattle traits. Table 2 presents the portions of weaning weight, postweaning gain, and yearling weight variation due to differences among Angus and Hereford herds as given by Wilson et al. (1972). Burfening et al. (1982) estimate that 16% of calving ease variation and 24% of birth weight variation is associated with

Table 2. Percent of phenotypic variance due to herd differences[a]

Trait	Breed	
	Angus	Hereford
Weaning weight	36.4	60.3
Postweaning gain	18.4	47.9
Yearling weight	26.6	19.6

[a]From Wilson et al. (1972).

differences among Simmental herds.

Cundiff et al. (1975) attribute 50% of weaning weight and 26% of yearling weight variation to herd differences in Angus and Polled Hereford. They also estimate the heritabilities of these differences as -0.24 for weaning weight and 0.21 for yearling weight, stating that these estimates show herd differences to be important only when determining yearling weight breeding value. However, the sample on which these estimates were based was rather small, consisting of 15 Angus bulls used in 18 herds and 44 Polled Hereford bulls used in 18 herds.

The three possible approaches to handling differences among herds are examined in a theoretical study by Spike and Freeman (1977) who evaluate accuracies for selection indices based on three types of records. The results of this study are reproduced in Table 3. Except in one case, the accuracy from using records with only herd environmental differences removed is the greatest. In the case of an extensive progeny test, using records with no herd differences removed produces equal accuracy, but removing all herd differences creates bias and

Table 3. Accuracies of different breeding value estimates using three types of records[a]

Source of records	Types of records		
	I[b]	II[c]	III[d]
Individual	0.50	0.52	0.58
10 progeny	0.63	0.63	0.69
100 progeny	0.99	0.93	0.99
Individual + 10 PHS[e]	0.55	0.57	0.63
Individual + 1000 PHS	0.63	0.62	0.68

[a]From Spike and Freeman (1977).

[b]Deviated from the population mean (no herd differences removed).

[c]Deviated from the herd mean (all herd differences removed).

[d]Deviated from the adjusted herd mean (only herd environmental differences removed).

[e]Paternal half-sibs.

lowers accuracy. This same bias is also seen when large numbers of paternal half-sib records are available.

Bereskin and Freeman (1965) show a large reduction in the herd-year-season variance component as a fraction of the variation within herd-year-season groups when computing selection indices from records deviated from a herdmate average adjusted for genetic differences among groups; however, the appropriate adjustment for intraherd mixed-model evaluations has not yet been clarified. Dairy industry programs based on Henderson's (1975b) intraherd model assume that all herd differences are environmental and Bolgiano et al. (1980) and Schaeffer et al.

(1982) conclude that this assumption of a common genetic base has little effect on interherd comparisons.

McMaster (1982) proposes a scheme to establish a common reference to tie intraflock ram and ewe evaluations. His plan is to simultaneously breed rams used by participating flocks to an unselected control flock. Intraflock breeding values could then be adjusted for the difference in ram evaluations between breeder and control flocks. He notes that expense is one drawback to this proposal.

An approach similar in intent to the above is possible if interherd NSE results are available. This approach is attempted by Nielsen (1974) and Schaeffer et al. (1980), investigating intraherd beef sire evaluation, and depends on the fact that interherd mixed-model evaluations properly account for herd genetic differences, as shown, for example, by Spike (1975), Bolgiano et al. (1980), and Boyle et al. (1983). In slightly different manners, both Nielsen (1974) and Schaeffer et al. (1980) adjust intraherd predictors by adding the difference between the interherd and intraherd predictors for sires appearing in both evaluations. One problem with this procedure is that the intraherd predictors for these sires would take on the interherd values without permitting any deviation for intraherd information not used in the interherd evaluation. Another, and possibly more serious, problem is that the differences between the two sets of predictors arising from accuracy differences are not taken into consideration. In other words, the interherd predictors will often be based on more records and would differ from the intraherd predictors even if the two bases were

identical since the intraherd predictors would be regressed further towards the base.

Incorporation of extrinsic information

The accuracy of intraherd evaluations may be enhanced by including information on related individuals in other herds through the incorporation of suitably weighted interherd sire predictors. The USDA was the first to try this enhancement in an industry program, including sire transmitting abilities in the computation of the USDA-DHIA cow indices (ARS, 1976).

The mixed-model technique for incorporating sire predictors is given, without derivation, by Henderson (1975b) as part of his intraherd evaluation method. A short description of the method is given here; two alternate derivations are provided by Quaas (1979) and VanVleck (1982). First, some weighting factor, n, is added to the diagonal element of the sire's intraherd equation to account for the quantity of information represented by the predictor to be incorporated. This weighting is conceptually such that n calves in a single contemporary group would produce the same accuracy of evaluation as that associated with the sire's interherd predictor. Since this number would be difficult to ascertain, n must be approximated, usually from the information published in the sire summary. One approximation is $(\sigma_e^2/PEV) - \alpha$, where PEV is the published prediction error variance, σ_e^2 is the error variance used to compute PEV, and α is the ratio of error to sire variance used to augment the interherd equations. If some or all of the sire's intraherd progeny records were also used in the interherd

evaluation, then n must be reduced by the contribution of these records to the interherd diagonal. After weighting the sire's diagonal, the sire's interherd predictor is multiplied by $2(n + \alpha)$ and the result is added to the sire's right-hand side. The factor 2 is required because the intraherd model predicts breeding value rather than transmitting ability. Schaeffer et al. (1980), Van Vleck (1982), and Schaeffer (1983) claim that this incorporation has the effect of adjusting the intraherd base to the interherd base, but Henderson (1975b) is careful to assert that the technique is not strictly valid if the bases differ.

Two reports study the incorporation of interherd sire information in beef prediction problems. Schaeffer et al. (1980) state that the reduction in prediction error is trivial when field-data evaluation predictors for reference sires are incorporated in the Canadian Simmental Association's designed evaluation. However, they comment that the effort required to achieve the reduction is also trivial. Skaar (1983) works with the yearling weights of 106 Hereford bull calves on central test and includes information on the calves' sires in three of the seven prediction methods studied. One of the three was an index prediction; one was a single-trait mixed model, and one was a multiple-trait mixed model that included calf hip height as an indicator trait. He concludes that the index and single-trait mixed-model predictors are equally capable of ranking the calves properly. However, calves placed on central test are often a highly selected group. This casts doubt on the assumption of a common base for the calf and sire information as well as on the applicability of using sire predictors intended to predict the average performance of a randomly chosen group of calves.

While the literature considers only the incorporation of sire predictors, the incorporation of cow predictors from other intraherd evaluations should be possible with the same technique, assuming a suitable base adjustment. This would overcome many of the disadvantages Schaeffer et al. (1982) list for intraherd cow evaluation, aiding, for example, the recovery of progeny data for a cow purchased after calving in another herd. Another possible application might be to reverse the process, as suggested by Cassel et al. (1983), and use intraherd dam predictors as covariates in NSE models to adjust for preferential mating bias.

Simulation Pilot Studies

Fraser (1957) was the first animal geneticist to publish results based on data generated with Monte Carlo techniques. The use of simulated data for pilot studies was, however, practiced well before this publication (e.g., McGilliard, 1952).

Miller (1979) criticizes simulation studies as especially error prone because of the many assumptions required to emulate complex biological systems. Henderson (1975a) also notes problems with simulation studies in his discussion of means for investigating sire evaluation models. He states that much effort is required to get other than "sketchy or trivial" results, but he supports the use of simulation for the study of new techniques, holding that the primary function of field-data research should be to explore and define populations and develop realistic models.

Limitations on the breadth of influence are not solely a characteristic of simulation studies, as Miller (1979) admits; the problems with biased samples can be seen in field-data reports such as Kress et al. (1977) and Skaar (1983). Extravagant interpretation is to be avoided regardless of the source of the data. The use of simulated data has become a common and accepted procedure for the study of mixed-model methodology (e.g., Everett et al., 1967; Pollak and Quaas, 1981; Famula and Van Vleck, 1982; Boyle et al., 1983).

METHODS

Data Generation

The data used in this study were simulated using modified versions of two programs described by Middleton (1981). The ECHO program simulates the breeding of beef cattle, generating genetic and phenotypic records for bulls, cows, and calves grouped in herds. Each run uses selection and mating choices made by each herd owner from a herd summary printout to emulate a cycle of breeding and calving for each herd. ECHO simulates five multiply-correlated traits: birth weight, weaning weight (direct and maternal), postweaning average daily gain, yearling hip height, and yearling weight. A companion program, SEP, performs a mixed-model interherd sire evaluation using records and control information output by ECHO.

A primary goal of the simulation process was to mimic field-data records as closely as possible, subject to the constraints imposed by the goals of this investigation. Thus, the sizes of the herds to be generated and their proportions in the population were chosen on the basis of the distribution of records in the Polled Hereford field data used to perform the 1983 sire evaluation. Eighteen herds were generated with 50 cows, 50 yearlings, and five sires. Two herds were generated with 150 cows, 150 yearlings, and 15 sires. The initial calf crop for each herd was generated by randomly mating each base sire to 10 base cows. The population parameters which controlled the generation of records are given in Tables 4 to 6. No yearling weight parameters are given because this trait is not directly generated, but is computed

Table 4. Phenotypic means

Trait	Mean
Birth weight	34 kg
Weaning weight	195 kg
Postweaning average daily gain	0.9 kg/day
Yearling hip height	114 cm

Table 5. Genetic and environmental standard deviations

Source of variation	Trait				
	BWT[a] (kg)	WWT[b] (kg)	MWWT[c] (kg)	PWG[d] (kg/day)	YHH[e] (cm)
Genetic	2.63	11.85	9.68	0.09	4.29
Temporary direct environment	3.23	12.92	6.81	0.11	3.51
Temporary herd environment	0.32	1.29	–[f]	0.01	0.35
Permanent maternal environment	–	–	9.70	–	–

[a]Birth weight.

[b]Direct weaning weight.

[c]Maternal weaning weight.

[d]Postweaning average daily gain.

[e]Yearling hip height.

[f]Not modeled.

Table 6. Correlations and heritabilities[a]

Trait	Trait				
	BWT[b]	WWT[c]	MWWT[d]	PWG[e]	YHH[f]
BWT	0.40	0.54	0	0.62	0.43
WWT	0.38	0.30	-0.64	0.50	0.65
MWWT	0	-0.40	0.20	0	0
PWG	0.23	0.22	0	0.40	0.75
YHH	0.41	0.36	0	0.27	0.60

[a]Genetic correlations are above the diagonal; phenotypic correlations are below the diagonal; heritabilities are on the diagonal.

[b]Birth weight.

[c]Direct weaning weight.

[d]Maternal weaning weight.

[e]Postweaning average daily gain.

[f]Yearling hip height.

as the sum of weaning weight and postweaning gain.

The 20 initial herd summaries, containing phenotypic information and intraherd breeding value estimates (index estimates) for all five traits, were distributed to volunteer herd owners. The use of volunteers was expected to provide records corresponding to field data produced under a variety of breeding programs. In other words, this was an attempt to avoid the biases possible when choosing a set of designed programs to simulate.

The birth year of the initial calf crop was considered year 2,

and the herd owners made four rounds of selection and mating, producing calf crops born in years 3, 4, 5, and 6. Herd owners with 50-cow herds were permitted to use up to five sires each year, and owners with 150-cow herds were permitted 15 sires. All owners were instructed to use at least two sires to insure that all records from each contemporary group would contribute to the sire evaluation.

All owners were also constrained to use at least one AI sire each round so that all herds would be tied. The strength of the tie was at the discretion of each herd owner. The use of one AI sire in a single round would have been satisfactory except that SEP does not use relationship ties. To insure that the base sires in all herds had progeny directly compared with AI sire progeny, owners were also instructed to reuse at least one of their base sires in the first round. Thus, the two-sire minimum had to be met by a combination of one AI and one non-AI base sire. In later rounds, owners could use either two AI sires or one AI and one non-AI sire.

For convenience, the AI sires offered were chosen from those offered to an educational group running the simulation at the same time. A stud of five sires was made available for each round. These sires generally had strengths in different traits in order to support a variety of selection programs. Before each round, except the first, the two least-popular sires were replaced. In addition to these 11 sires, an additional AI sire was reserved for the use of two volunteers who wished to attempt to influence the sire evaluation results through an elaborate preferential mating plan. This was allowed in order to

gauge the effect of such practices on the results of this investigation.

For simplicity in constructing multiple sets of single-trait equations, SEP uses only records for calves which live to a year of age. The first sire evaluation, therefore, was not performed until year 4, when the first calves by AI sires, born in year 3, reached a year of age. Thus, the first evaluation included the records for yearlings born in years 2 and 3. Three subsequent evaluations were performed, sequentially adding records for yearlings born in years 4, 5, and 6.

For each trait to be evaluated, SEP constructs a set of single-trait mixed-model equations with contemporary (herd-year) groups absorbed and sires grouped on birth year. AI sires were grouped with the yearling sires first available in the year the AI sires were introduced. For example, the initial five AI sires were grouped with the base yearlings. Because only yearling records are used, each set of equations differs only in the right-hand sides and in the variance ratio used to augment the sire diagonal elements. The variance ratios used in this study are presented in Table 7. Whereas the true breeding values simulated for each animal are expressed in relation to a fixed base, the group equations were restricted before solution to express all groups relative to the group of base sires. The sets of equations were solved using 30 rounds of Gauss-Seidel iteration, described by Van Norton (1959), as modified to use the block iteration technique described by Vargas (1962).

Table 7. Variance ratios used for sire evaluation

Trait	Ratio
Birth weight	9
Weaning weight	12
Postweaning average daily gain	9
Yearling hip height	6
Yearling weight	9

Estimation of Herd Adjustments

Whereas BLUP sire evaluation properly accounts for the genetic differences among herds, as related in the literature review, the recovery of these differences from the sire evaluation equations and solutions should be possible. If so, the estimates of these differences would be relative to a common base and could be used to adjust the bases of corresponding intraherd evaluations to permit fair interherd comparisons.

Harvey (1975) describes the process of backsolving a set of equations for absorbed fixed effects. This process can be used to derive a means of computing estimates of genetic herd differences. The derivation is based on the following sire evaluation model:

$$y_{ijk\ell} = \mu + h_i + c_{ij} + s_k + e_{ijk\ell},$$

where $y_{ijk\ell}$ = the record of calf ℓ by sire k in contemporary group j in herd i,

μ = the population mean,

h_i = the fixed environmental effect of herd i, i = 1 ... p,

c_{ij} = the fixed environmental effect of the jth contemporary group in herd i, j = 1 ... q_i,

s_k = the random genetic effect of sire k, k = 1 ... r, and

$e_{ijk\ell}$ = the random error associated with an observation.

For analysis, the fixed effects are usually combined into classes and absorbed. Let

$$d_{ij} = \mu + h_i + c_{ij}.$$

Then, the model can be given as

$$y_{ijk\ell} = d_{ij} + s_k + e_{ijk\ell},$$

or, in matrix notation, as

$$y = Xd + Zs + e,$$

where y, d, s, and e are vectors of observations, fixed effects, random effects, and errors, respectively. The matrices X and Z are known incidence matrices relating the corresponding vectors to the observation vector. The full mixed-model equations (MME) constructed from this model are as follows:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha \end{bmatrix} \begin{bmatrix} \hat{d} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix},$$

where A^{-1} = the inverse of the assumed numerator relationship matrix among sires, and

α = the ratio of error to sire variance.

The MME with the $\hat{d}$ equations absorbed are

$$(Z'SZ + A^{-1}\alpha)\hat{s} = Z'Sy,$$

where $S = I - X(X'X)^{-1}X'$.

Once the vector $\hat{s}$ is obtained, the solutions to the absorbed equations are computed as

$$\hat{d} = (X'X)^{-1}(X'y - X'Z\hat{s}). \qquad (1)$$

The herd environment solutions can be extracted from $\hat{d}$ after this back-solution, but a restriction must first be imposed. A convenient restriction in this instance is

$$\sum_i n_{i\ldots}\hat{h}_i = \sum_j n_{ij\cdot\cdot}\hat{c}_{ij} = 0,$$

where the subscripted values of n represent the number of observations in a subclass. Now,

$$\hat{\mu} + \hat{h}_i = 1/n_{i\ldots}\,(\sum_j n_{ij\cdot\cdot}\hat{d}_{ij}). \qquad (2)$$

Further decomposition of Equation 2 is not necessary; the herd genetic merit for a herd, say m, can be estimated as a deviation from the NSE base by removing this environmental portion from the herd mean, say $\bar{H}_i$:

$$\hat{m}_i = \bar{H}_i - (\hat{\mu} + \hat{h}_i). \qquad (3)$$

This result can be manipulated into a clearer form that does not require calculation of the herd means. Expressing Equation 1 in

summation notation,

$$\hat{d}_{ij} = 1/n_{ij..}(y_{ij..} - \sum_k n_{ijk.}\hat{s}_k). \qquad (4)$$

Substituting Equation 4 into Equation 2 yields

$$\hat{\mu} + \hat{h}_i = 1/n_{i...}(\sum_j (n_{ij..}/n_{ij..})(y_{ij..} - \sum_k n_{ijk.}\hat{s}_k)),$$

which reduces to

$$\hat{\mu} + \hat{h}_i = 1/n_{i...}(y_{i...} - \sum_j \sum_k n_{ijk.}\hat{s}_k). \qquad (5)$$

Also,

$$\bar{H}_i = y_{i...}/n_{i...}, \qquad (6)$$

and substituting Equations 5 and 6 into Equation 3 yields

$$\hat{m}_i = 1/n_{i...}(y_{i...} - y_{i...} + \sum_j \sum_k n_{ijk.}\hat{s}_k).$$

This reduces to

$$\hat{m}_i = (\sum_j \sum_k n_{ijk.}\hat{s}_k)/(n_{i...}). \qquad (7)$$

In other words, the herd merit estimate is simply a weighted average of the solutions for those sires with progeny records in the herd.

The relationship of this calculation to the sire evaluation equations can be seen more clearly in matrix notation. For each herd, envision a vector, J_i, with q_i rows (q_i being the number of contemporary groups in herd i) that each contain the reciprocal of the number of records contributed to the sire evaluation by the herd; i.e.,

$$J = \begin{bmatrix} 1/n_{i\ldots} \\ 1/n_{i\ldots} \\ \vdots \\ 1/n_{i\ldots} \end{bmatrix}.$$

Now let K be a matrix constructed from these vectors:

$$K = \begin{bmatrix} J_1' & & [\text{null}] \\ & J_2' & \\ & & \ddots \\ [\text{null}] & & J_p' \end{bmatrix},$$

and let L be the product KX'Z. This matrix L is easily constructed during the process of building the MME, and Equation 7 becomes

$$\hat{m} = L\hat{s}. \tag{8}$$

The calculation process is similar when sires are nested in groups. If the grouping model is given as

$$y = Xd + Q'Zq + Zs + e,$$

where q is the vector of fixed genetic group effects related to sires by Q and to observations by Z, then the sire predictors, say $\hat{u}$, are calculated as

$$\hat{u} = Q\hat{g} + \hat{s}.$$

The L matrix in this circumstance is constructed exactly as before; the only change to Equation 8 is the substitution of the vector $\hat{u}$ for $\hat{s}$.

That $\hat{m}$ is not a value useful for ranking herds should be emphasized;

$\hat{m}$ is a determination of that genetic component that is common to the records produced in a single herd and that is not estimable when the records are analyzed using an intraherd procedure. To make this distinction is important because the estimates for herds beginning performance recording at different times would likely differ even if the herds were of similar merit. In other words, $\hat{m}$ does not correspond to a determinable fixed point in time for a herd, nor do the estimates necessarily occupy equivalent positions on the trend lines for different herds.

This is not to say that no value can be calculated on which herds can be ranked. Herds can be compared using any value associated with a fixed point in time, such as the average adjusted breeding value for all progeny born in a given year.

Before applying $\hat{m}$ to the adjustment of intraherd predictors, all of the values in the vector must be doubled. This is required because $\hat{m}$ is derived from sire transmitting abilities but is to be applied to predictors of breeding value. The doubled values, say $\hat{m}^*$, could also be produced by doubling the vector $\hat{s}$ (or $\hat{u}$) before making the calculation in Equation 8. The adjustment is then simply the addition of $\hat{m}_i^*$ to each predictor resulting from the intraherd evaluation of herd i. For this to work properly, however, the intraherd evaluation must be performed with a floating base, representing an unknown component common to all animals in the herd and not just that group chosen as the base in a fixed-base procedure. The values of $\hat{m}$ themselves may be relative to a fixed or floating base NSE, and the adjusted predictors will be based accordingly.

One advantage of this method over those using the difference between

interherd and intraherd sire predictors is that $\hat{m}$ depends only on the more-accurate NSE values and the relative contribution of each sire to a herd. The value of $\hat{m}$ is independent of herd size and the differing accuracy levels of sire predictors from the two sources: herds using the same sires in the same proportions are estimated as being of the same merit regardless of herd size differences.

This dissertation treats $\hat{m}$ as an isolated phenomenon. Such treatment may tend to distort perspective. It must be kept in mind that $\hat{m}$ is of little interest alone; the sole worth of this value is as an adjustment which allows the results of independent, intraherd, mixed-model evaluations to approximate the predictors produced by solving a single set of mixed-model equations incorporating all animals in a breed. A possible industry scenario is described in the section on applications.

Study of Herd Adjustments

While all five simulated traits were available to the herd owners to use in the design of their breeding programs, only one trait, post-weaning average daily gain (PWG), was investigated. This trait was chosen for three reasons:

1) PWG represents a growth trait of medium to high heritability and of economic importance to beef producers;

2) PWG is free of any estimation problems associated with compound traits such as weaning or yearling weight; and

3) PWG is measured only on those animals that contribute records to the simulated sire evaluation.

Values of $\hat{m}^*$ for each herd were obtained from each of the four sire evaluations. The corresponding true value for each herd, m^*, was calculated as the average true PWG breeding value for all animals whose records were used in the sire evaluation. The correctness of $\hat{m}^*$ in relation to m^* was measured by absolute error (AE):

$$AE = |m^* - \hat{m}^*|.$$

This error was appraised with a variety of regression and correlation techniques, which are described with the associated results in the next section. The effect of herd size on AE and the change in AE between evaluations were of interest, and of particular interest was the relationship of error to five variables chosen to measure the strength of the ties among the herds. Finally, in addition to AE, the ability of $\hat{m}^*$ to properly represent the differences among herds was studied.

RESULTS

Data Description

After each sire evaluation, nine values were calculated for each herd.

Five of the variables were intended to measure the strength of the tie between the herd and the rest of the population based on the herd's use of tie (AI) sires. These are identified as follows:

1) TPY = the average number of tie sires used per year;

2) TTS = the total number of different tie sires sampled;

3) PTR = the percent of progeny records by tie sires;

4) RNT = the average yearly ratio of nontie to tie sires; and

5) TTE = the total tie-sire effective progeny number from the sire evaluation.

Two of the remaining variables are the true and estimated herd PWG adjustment factors (TA and EA, corresponding to m^* and $\hat{m}^*$), and the last two are the true herd rank (TR) and estimated herd rank (ER). While the previous section emphasized that the herd adjustments are not generally useful for ranking herds, the ranks are useful in this instance because all herds have the same number of years of records and maintained the same herd size. Rank ties were handled by assigning tied herds the average of the higher and lower ranks.

The data resulting from these calculations are given in Tables 8 to 11.

The importance of the true herd adjustments can be judged against the standard deviation of TA. Since the genetic standard deviation of

Table 8. Herd information from first evaluation

Herd[a]	TPY	TTS	PTR	RNT	TTE	TA (kg)	EA (kg)	TR	ER
1	2	2	24	1.50	134	0.045	0.041	3.5	8.5
2	4	4	43	0.25	225	-0.018	-0.009	20.0	19.0
3	1	1	11	3.00	67	0.054	0.036	2.0	11.5
4	1	1	20	2.00	95	0.023	0.050	13.0	3.0
5	1	1	10	4.00	95	0.036	0.041	8.0	8.5
6	1	1	8	4.00	67	0.027	0.045	11.5	5.5
7	2	2	16	1.00	134	0.068	0.059	1.0	1.0
8	1	1	11	4.00	95	0.041	0.050	5.5	3.0
9	2	2	34	1.00	70	-0.014	-0.005	19.0	18.0
10	4	4	14	0.50	232	0.018	0.032	15.0	13.0
11	2	2	35	0.50	134	0.009	0.041	18.0	8.5
12	2	2	32	1.00	130	0.018	0.005	15.0	17.0
13	3	3	31	0.67	190	0.036	0.036	8.0	11.5
14	2	2	32	1.00	151	0.036	0.041	8.0	8.5
15	1	1	16	3.00	95	0.018	0.045	15.0	5.5
16	1	1	14	1.00	56	0.032	-0.014	10.0	20.0
17	1	1	16	1.00	56	0.045	0.018	3.5	16.0
18	1	1	20	1.00	56	0.014	0.023	17.0	15.0
19	2	2	26	1.50	130	0.041	0.027	5.5	14.0
20	3	3	19	1.60	225	0.027	0.050	11.5	3.0

[a]Herds 1 to 18 are 50-cow herds; herds 19 and 20 are 150-cow herds.

Table 9. Herd information from second evaluation

Herd[a]	TPY	TTS	PTR	RNT	TTE	TA (kg)	EA (kg)	TR	ER
1	2	3	33	1.25	412	0.059	0.073	6.0	8.5
2	5	7	63	0.13	692	0.009	0.041	19.0	16.0
3	2	2	21	2.25	340	0.064	0.068	4.0	10.5
4	2	2	27	1.75	350	0.041	0.073	13.0	8.5
5	1	2	13	4.00	340	0.045	0.041	11.0	16.0
6	1	2	11	4.00	340	0.054	0.064	8.0	12.0
7	2	3	27	1.00	389	0.082	0.100	1.0	2.0
8	2	2	34	2.50	350	0.064	0.104	4.0	1.0
9	1	2	44	1.50	122	-0.023	-0.014	20.0	20.0
10	4	5	19	0.50	594	0.018	0.045	18.0	14.0
11	2	3	42	0.75	389	0.036	0.086	14.5	4.0
12	3	4	54	0.50	535	0.045	0.068	11.0	10.5
13	2	5	42	0.59	507	0.064	0.086	4.0	4.0
14	2	3	43	1.00	445	0.054	0.077	8.0	7.0
15	1	1	21	2.50	218	0.036	0.059	14.5	13.0
16	1	1	19	1.00	95	0.032	-0.009	16.0	19.0
17	1	1	23	1.00	95	0.054	0.023	8.0	18.0
18	1	1	32	1.00	95	0.027	0.041	17.0	16.0
19	3	4	40	1.09	535	0.068	0.086	2.0	4.0
20	3	4	24	1.84	535	0.045	0.082	11.0	6.0

[a]Herds 1 to 18 are 50-cow herds; herds 19 and 20 are 150-cow herds.

Table 10. Herd information from third evaluation

Herd[a]	TPY	TTS	PTR	RNT	TTE	TA (kg)	EA (kg)	TR	ER
1	2	4	33	1.50	552	0.077	0.100	4.5	8.0
2	5	9	72	0.08	1023	0.032	0.077	16.0	14.0
3	2	3	27	1.83	508	0.068	0.082	8.0	12.5
4	2	3	30	1.67	550	0.059	0.100	12.5	8.0
5	1	2	15	4.00	424	0.059	0.068	12.5	15.0
6	1	3	14	4.00	659	0.064	0.091	10.5	10.5
7	2	4	36	0.89	589	0.104	0.122	1.0	2.0
8	2	3	47	1.83	574	0.086	0.136	2.0	1.0
9	2	2	36	2.33	157	-0.018	0	20.0	19.0
10	3	5	18	0.83	816	0.009	0.050	18.0	16.0
11	2	3	40	1.50	529	0.064	0.109	10.5	5.0
12	2	6	68	0.33	866	0.073	0.109	6.0	5.0
13	2	6	36	1.06	707	0.068	0.091	8.0	10.5
14	2	4	51	1.00	645	0.082	0.109	3.0	5.0
15	1	2	31	2.33	315	0.054	0.082	14.0	12.5
16	1	3	38	0.67	326	0.023	-0.009	17.0	20.0
17	1	3	42	0.67	326	0.041	0.014	15.0	18.0
18	1	3	48	0.67	326	0.005	0.018	19.0	17.0
19	2	5	39	1.39	806	0.077	0.100	4.5	8.0
20	2	5	43	1.22	806	0.068	0.118	8.0	3.0

[a]Herds 1 to 18 are 50-cow herds; herds 19 and 20 are 150-cow herds.

Table 11. Herd information from fourth evaluation

Herd[a]	TPY	TTS	PTR	RNT	TTE	TA (kg)	EA (kg)	TR	ER
1	2	6	36	1.38	877	0.100	0.113	6.5	11.0
2	5	11	78	0.06	1457	0.059	0.113	16.0	11.0
3	2	4	27	2.13	622	0.082	0.104	9.5	13.0
4	2	5	33	2.00	958	0.082	0.118	9.5	8.5
5	1	3	23	3.50	811	0.073	0.095	12.5	15.0
6	1	3	23	3.50	811	0.082	0.113	9.5	11.0
7	3	5	43	0.75	909	0.113	0.145	1.0	3.0
8	2	5	58	1.38	980	0.104	0.150	2.0	2.0
9	2	4	42	2.00	694	0	0.032	20.0	19.5
10	3	6	29	0.71	1118	0.018	0.050	19.0	17.5
11	2	3	38	1.88	681	0.073	0.127	12.5	6.5
12	3	7	73	0.25	1215	0.091	0.136	6.5	4.0
13	2	7	38	0.92	1004	0.082	0.100	9.5	14.0
14	2	5	58	0.83	965	0.095	0.127	4.5	6.5
15	1	2	37	2.00	398	0.068	0.118	14.0	8.5
16	2	5	50	0.50	805	0.041	0.032	17.0	19.5
17	2	5	54	0.50	805	0.064	0.050	15.0	17.5
18	2	5	58	0.50	805	0.032	0.054	18.0	16.0
19	3	6	45	1.21	1072	0.100	0.132	3.0	5.0
20	2	7	54	0.92	1215	0.095	0.159	4.5	1.0

[a]Herds 1 to 18 are 50-cow herds; herds 19 and 20 are 150-cow herds.

individual PWG records is 0.09 kg, and since the smallest number of records contributed by a herd in the first evaluation is 87, then the standard deviation of TA is less than or equal to 0.009 kg for all herds in all evaluations. In the first evaluation alone, 17 of the 20 herds differ from the base by double this value or more.

Perhaps a better way to determine the consequences of ignoring herd differences is by examining the economic impact. Unfortunately, this is not an easy determination. To take a simple case, however, assume that a bull is expected to produce 100 market progeny during his productive span. Then failing to account for a herd deviation of $\pm$ 0.018 kg would over- or underestimate the total gain of his progeny by 1.8 kg/day, or 228 kg for the 160-day postweaning period, compared to 100 progeny from an average bull from a herd with a 0 deviation. Assuming the live-weight price of fed calves to be \$0.27/kg, the calculated economic worth of the bull would be mistaken by $\pm$ \$78.00 if the herd adjustment were ignored. Therefore, differences of $\pm$ 0.018 kg or more might well influence the decisions of commercial bull buyers, or buyers of bulls to be used in producing commercial bulls.

A second data set, used to test the ability of EA to measure herd differences, was created by randomly pairing the herds after each evaluation and computing the true and estimated differences between each pair: $TA_i - TA_j$ and $EA_i - EA_j$. These paired comparisons are presented in Tables 12 to 15.

Another indicator of the importance of accounting for the herd differences can be gleaned from the paired comparisons. The error arising from ignoring a true difference is the magnitude of the

Table 12. Paired comparisons for first evaluation

Herd 1	Herd 2	$TA_1 - TA_2$ (kg)	$EA_1 - EA_2$ (kg)
1	15	0.027	-0.005
13	2	0.054	0.045
3	17	0.009	0.018
5	4	0.014	-0.009
19	6	0.014	-0.018
7	18	0.054	0.036
8	20	0.014	0
14	9	0.050	0.045
10	11	0.009	-0.009
16	12	0.014	-0.018

Table 13. Paired comparisons for second evaluation

Herd 1	Herd 2	$TA_1 - TA_2$ (kg)	$EA_1 - EA_2$ (kg)
1	5	0.014	0.032
16	2	0.023	-0.050
3	20	0.018	-0.014
4	15	0.005	0.014
6	17	0	0.041
7	8	0.018	-0.005
18	9	0.050	0.054
12	10	0.027	0.023
13	11	0.027	0
19	14	0.014	0.009

difference, and, in all but a few pairings, this error is greater than the error from using the estimates, calculated as $(TA_i - TA_j) - (EA_i - EA_j)$.

Table 14. Paired comparisons for third evaluation

Herd 1	Herd 2	$TA_1 - TA_2$ (kg)	$EA_1 - EA_2$ (kg)
1	17	0.036	0.086
12	2	0.041	0.032
3	16	0.045	0.091
19	4	0.018	0
7	5	0.045	0.054
13	6	0.005	0
8	20	0.018	0.018
15	9	0.073	0.082
14	10	0.073	0.059
11	18	0.059	0.091

Table 15. Paired comparisons for fourth evaluation

Herd 1	Herd 2	$TA_1 - TA_2$ (kg)	$EA_1 - EA_2$ (kg)
3	1	0.009	-0.005
14	2	0.036	0.014
12	4	0.009	0.018
5	9	0.073	0.064
20	6	0.014	0.045
7	10	0.095	0.095
8	15	0.036	0.032
11	17	0.009	0.077
13	16	0.041	0.068
19	18	0.068	0.077

Size and Trend Analyses

The effects of herd size and successive evaluations on absolute error (AE, calculated as $|TA - EA|$) were initially investigated with a split-plot analysis of variance. This analysis is summarized in Table 16. To insure a conservative F test for evaluation and the

Table 16. Effects of herd size and evaluation on absolute error

Source	df[a]	MS
Herd size	1	0.0019
Herds/size[b]	18	0.0019
Evaluation	3 (1)	0.0041*
Evaluation x size	3 (1)	0.0003
Evaluation x herds/size[c]	54 (18)	0.0004

[a]Values in parentheses are the conservative degrees of freedom used for F tests. See text for explanation.

[b]Error for testing herd size.

[c]Error for testing evaluation and evaluation*size.

*$p < 0.01$.

evaluation x size interaction, the F ratios were compared with critical values of F as if the ratios had considerably fewer degrees of freedom. The conservative degrees of freedom were obtained by dividing the degrees of freedom for the last three effects in Table 16 by the evaluation degrees of freedom.

The results of this analysis indicate that AE is not dependent on herd size, while there are highly significant changes in AE with time. The insignificance of herd size shows, within the ranges represented in this study, that the ability of EA to reflect TA is not altered by differing numbers of sires nor by differing numbers of records.

Extension of this finding beyond this simulation should be approached with care. If the inverse of the sire evaluation coefficient matrix could be had, then the accuracy of EA could be computed as

$$V(EA) = LV(S)L',$$

where V(S) is the variance-covariance matrix of sire breeding values. The variance-covariance matrix of EA for this study would be heavily weighted by the contribution of the AI sires. Thus, the accuracy of EA would bear little relation to herd size because the proportionate use of AI sires was not related to herd size. In real populations, the general accuracy levels of the sires used might be associated with differing breeding programs in herds of different sizes.

Studies of field data are required to clarify this matter, but an indication of the possibilities is given by Hudson et al. (1980). This work dealt with factors influencing progeny-test accuracies in designed sire-evaluation programs. Herd size was found to have a marked influence on accuracy because the connectedness of bulls tested in larger herds was increased.

Having discounted the effect of herd size, the trends in AE, TA, and EA were examined in more detail. As shown by the AOV summaries in Tables 17 to 19, the higher-order polynomial effects were not significant; the trends for all three measures were strictly linear. The linear trend in AE is approximately the difference between the EA and TA trends.

Examining the differences between the sire-evaluation predictors and the true sire breeding values reveals that the predictors become more accurate over time, yet AE actually increases over the span. The key to understanding the seeming contradiction lies in noting that the EA trend is a function of the trend in the group of sires used each year while the lower TA trend is a function of the change in the total

Table 17. Analysis of trend in absolute error

Source	Df	MS
Evaluation	3	0.0057
Linear[a]	1	0.0169*
Quadratic	1	0.0003
Lack of fit	1	0
Residual	76	0.0008

[a]Trend estimate is 0.006 kg/year.

*$p < 0.01$.

Table 18. Analysis of trend in true herd adjustment

Source	Df	MS
Evaluation	3	0.034
Linear[a]	1	0.100*
Quadratic	1	0
Lack of fit	1	0
Residual	76	0.003

[a]Trend estimate is 0.014 kg/year.

*$p < 0.01$.

population of breeding animals. Therefore, the sire trend must substantially exceed the dam trend.

As stated by Harville and Henderson (1967), the trends in sire and dam merit must, in theory, be equal in the long run. This statement probably holds for the merit of the replacement sires and dams available each year, but, due to differing replacement rates, this claim would not generally hold for the total breeding populations of sires and dams. Hintz et al. (1978), for example, shows that the trend for dairy cows

Table 19. Analysis of trend in estimated herd adjustment

Source	Df	MS
Evaluation	3	0.091
Linear[a]	1	0.273*
Quadratic	1	0
Lack of fit	1	0.001
Residual	76	0.006

[a]Trend estimate is 0.024 kg/year.

*$p < 0.01$.

evaluated in the Northeast is overestimated by the trend for AI sires in the Northeast AI Sire Comparison.

The trend difference, then, can be checked by inspecting the replacement rates for sires and dams.

The mean tenure for all sires was 1.4 years, and the mean tenure of AI sires alone was 2.0 years. For comparison, Kratz et al. (1977) found a 2.98-year mean tenure for U.S. and Canadian AI sires leaving service from 1970 to 1973; however, the mean within-herd tenure of Polled Hereford sires is 1.3 years in field data collected from 1966 to 1980 (Middleton, unpublished data, 1983, Dept. of Animal Science, Iowa State University).

The mean tenure for dams, on the other hand, was estimated as 3.7 years from the mean percent of the cow herd composed of yearling heifers in years 3 to 6. This is slightly lower than the 4- to 5-year generation interval usually assumed for beef females.

Another influence might also be responsible for an increase in AE. If widespread positive assortative or preferential mating were

practiced, the inflation of sire predictors could have the effect of increasing AE. This seemingly was not the case in this study because the predicted sire breeding values approached the true values over time rather than the reverse. But the effect of preferential mating might be an important factor in real populations; for example, Wilson (personal communication, 1983, Dept. of Animal Science, Iowa State University) states that the practice is common in purebred Angus herds.

A reduction in AE might be achieved by developing an adjustment to correct EA from a weighted average of the predictors for the maternal grandsires of calves providing records to the sire evaluation. An improved sire model, such as one which uses information on sire relationships, might also be of aid.

Tie Strength Analyses

The analyses described in this section were all performed separately for each evaluation for two primary reasons.

First, an attempt to pool the evaluations would require a weighted least-squares approach because the variance of AE is clearly changing with time. This variance would be inordinately difficult to estimate even if the inverse of the sire evaluation coefficient matrix were available, and the sample variance is probably not an acceptable approximation. Thus, the conservative approach seemed prudent.

Second, the possibility of an autocorrelated error structure could not be overlooked. SAS (1982b) delineates tests for such a structure

that use the autocorrelation among the residuals of predictions from the regression of AE on evaluation. The first-order autocorrelation was -0.115 and the Durbin-Watson d statistic was 2.15, which is indicative of a lack of autocorrelation. However, SAS (1982b) warns that the autocorrelation among residuals may not be a very good estimate of the true autocorrelation when the sample size is small. Again, the within-evaluation analysis was considered more prudent.

The obvious collinearities among the five tie-strength indicators made it necessary to first determine which sets of these variables could be modeled together. This determination was made using the collinearity diagnostic features described in SAS (1982b).

One of these features is the computation of variance inflation factors (VIF). The VIF are the amounts by which the variance of each estimated partial regression coefficient is inflated in comparison with a noncollinear model. These are computed as the reciprocal of $1 - R^2_{i \cdot 0}$, where $R^2_{i \cdot 0}$ is the multiple correlation coefficient of each variable with all others. The simultaneous use of all five variables produced VIF ranging from 2.0 to 11.7, which signifies that this model is to be avoided.

Another diagnostic feature, based on the eigenvalues and eigenvectors (principal component vectors) of X'X, allows the collinearities to be pinpointed more specifically. The eigenvalues are used to construct condition indices, which are the square roots of the ratios of the largest eigenvalue to the eigenvalues of X'X. The principal component vectors indicate the proportion of variation in each regression estimate that is accounted for by each principal component. A collinearity

problem arises when a principal component associated with a high condition index contributes strongly to the variance of two or more variables. The condition indices and eigenvectors for each evaluation are presented in Tables 20 to 23.

Table 20. Collinearity diagnostics from first evaluation

Principal component	Condition index	Variance portion				
		TPY	TTS	PTR	RNT	TTE
1	1.0	0	0	0.02	0.02	0.01
2	2.1	0	0	0.21	0.14	0.02
3	3.2	0	0	0.77	0.62	0.01
4	7.4	0	0	0	0.23	0.96
5	1933795.0	1.0	1.0	0	0	0

Table 21. Collinearity diagnostics from second evaluation

Principal component	Condition index	Variance portion				
		TPY	TTS	PTR	RNT	TTE
1	1.0	0.01	0.01	0.02	0.02	0.01
2	1.9	0.01	0.01	0.11	0.19	0.03
3	3.2	0.02	0	0.84	0.46	0
4	5.1	0.96	0.08	0	0.13	0.13
5	7.9	0	0.91	0.02	0.21	0.84

The variables were divided into two sets on the basis of these diagnostics using a somewhat intuitive approach. The variables TPY, TTS, and TTE comprised the first set, and PTR and RNT comprised the second. The variables in each set are those that should not be used in models together; thus, there were six models investigated, each composed of a variable drawn from each set. Subsequent collinearity

Table 22. Collinearity diagnostics from third evaluation

Principal component	Condition index	Variance portion				
		TPY	TTS	PTR	RNT	TTE
1	1.0	0.02	0.01	0.02	0.02	0.01
2	1.9	0.02	0	0.13	0.13	0.05
3	3.5	0.05	0	0.71	0.59	0.02
4	4.1	0.82	0.02	0.05	0.13	0.23
5	6.9	0.08	0.97	0.08	0.15	0.69

Table 23. Collinearity diagnostics from fourth evaluation

Principal component	Condition index	Variance portion				
		TPY	TTS	PTR	RNT	TTE
1	1.0	0.01	0.01	0.02	0.01	0.01
2	2.4	0.01	0.01	0.17	0.14	0.08
3	3.6	0.29	0	0.45	0.16	0.09
4	4.7	0.60	0.03	0.35	0.51	0.07
5	7.3	0.08	0.94	0.01	0.19	0.76

analyses of the six models showed that the variance inflation factors dropped to values of 1.9 or less.

The 24 resulting analyses of variance are not reproduced here because none of the models had any significant effect on AE despite apparently large differences in connectedness among the herds. Absolute error is evidently solely an expression of the gap between the sire and dam trends in each herd, as demonstrated in the preceding section, and the trends in each herd do not seem to be associated with choices involving the use of tie sires.

This result does not appear intuitively likely since it would imply that the error would be unchanged even if herds were totally unconnected.

Perhaps a minimum level of connectedness can be postulated instead, above which differences in connectedness would have only a trivial effect on AE. This would concur with the finding of Hudson et al. (1980), who conclude that conceptions by reference sires equal to 10% of the conceptions by young bulls in a designed progeny test are sufficient to make the accuracy of comparisons among young bulls dependent on other factors, such as the number of progeny by each young bull. If this postulate is so, and granting that this unknown minimum connectedness is exceeded by every herd in this study, then meeting this minimum requirement should not be difficult for most herds in real populations.

The establishment of a connectedness criterion is manifestly beyond the capability of this study, though it was hoped otherwise. Further work is needed, including, perhaps, the derivation of more appropriate measures of connectedness.

Herd Comparison Analyses

At first sight, the corollary of minimum AE is correctness of inter-herd comparisons. This seems obvious because of the extreme case: if AE is zero, then all herd comparisons are correct by definition. But this corollary is not necessarily so if AE is not associated in some predictable way with the merit of the dams in a herd. The reason for this concern is that in the first evaluation, EA is dependent on the predictors of the base sires to a large extent, which are constrained by the parameters to resemble the population of base dams but do not necessarily reflect dam merit on a herd-to-herd basis. In real popula-

tions, the sires and dams in a herd will nearly always bear some closer resemblance to one another than the average of the population. Additionally, the sire predictors are improving with time, implying that the accuracy of comparisons between sire predictors is improving and, therefore, that the accuracy of comparisons between estimated herd adjustments is improving, even though AE is increasing.

This anomaly was first investigated via the three types of correlation analysis detailed in SAS (1982a). These are the Pearson product-moment correlation, the Spearman rank correlation, and the Kendall rank correlation. The three types of correlations between TA and EA for each evaluation are presented in Table 24.

Table 24. Correlations between true and estimated herd adjustments

Evaluation	Pearson	Spearman	Kendall
1	0.56*	0.34	0.25
2	0.73*	0.70*	0.54*
3	0.86*	0.87*	0.72*
4	0.88*	0.85*	0.69*

*$p < 0.01$.

While the Pearson correlation between TA and EA was strong in all evaluations, the herd ranks based on TA and EA were uncorrelated in the first evaluation. The rank correlations strengthened considerably in later evaluations, and rank changes generally represented inconsequential differences of a few thousandths of a kilogram.

The decrease in the rank correlations between the third and fourth evaluation is not readily explicable. Possibly a plateau was reached at the third evaluation and further changes are simply due to sampling variation; too few evaluations were performed to settle this question.

A second approach to examining herd comparisons was taken via the paired-comparison t test. First, the differences between the true and estimated pair differences in Tables 12 to 15 were calculated:

$$DIFF = (TA_i - TA_j) - (EA_i - EA_j).$$

Then, the mean DIFF for each evaluation was tested under the null hypothesis DIFF = 0. Acceptance of the null hypothesis indicates that $EA_i - EA_j$ is an accurate representation of the true difference. The results of these tests are given in Table 25. Only in the first evaluation was DIFF significantly different from zero; this corresponds well with the results of the rank correlation analysis.

Judging from the results in this section, the variance-covariance matrix for EA would be a better indicator of the merit of the estimation technique than is AE. The method is not as poor as one might infer from the results of the AE analyses in previous sections; however, the reduction of AE is still desirable to insure that the sires in use accurately indicate the merit of the dam population.

These observations may raise more questions than they answer. For example, the use of more tie sires is clearly desirable since sires used in multiple herds typically have higher accuracies and would contribute more to the accuracy of EA. This would point to a strong relationship between connectedness and the accuracy of EA, though

Table 25. Paired-comparison t test results

Evaluation	Mean DIFF[a] (kg ± SE)	t[b]
1	0.017 ± 0.004	4.09*
2	0.009 ± 0.010	0.91
3	-0.010 ± 0.008	-1.30
4	-0.010 ± 0.008	-1.13

[a]All means based on 10 observations.

[b]Test for H_0: mean DIFF = 0.

*$p < 0.01$.

connectedness appears to have little influence on AE. Also, large herds have a distinct advantage in the intraherd testing of nontie sires because large herds could accumulate more records for each nontie sire and maintain a respectable EA accuracy in this way. Again, this implies the importance of a factor (herd size) that does not affect AE.

Most of the change in rank correlation with time is probably due to the shifting of the herd structures from randomly pooled groups to the more closely related groups found in real populations. Nevertheless, the question is also raised about the differences in the qualities of EA calculated for herds which have been keeping records for different lengths of time. This aspect also merits further study, though a minimum of two or three years would seem to be sufficient.

APPLICATIONS

The solution of a full set of mixed-model equations including all animals within a breed is perhaps not beyond the realm of possibility now, and such a procedure is certainly going to be possible in the near future given the rapid pace of developments in the computer sciences. The total number of equations to be solved is no different whether the herds are considered simultaneously or individually. The only difference is that a relatively small number of additional, extraherd, off-diagonal elements is considered in the simultaneous solution.

Yet the eventual use of the simultaneous approach is not expected, despite the advantages of analyzing the population as a unit, because this procedure would fail to meet the needs of beef breeders. The purebred producer must receive the latest report on his stock soon after submitting the records of his latest calf crop in order to use the information for selection decisions and marketing. Only the individual processing of herds can provide the flexibility to meet this goal.

Individual processing requires extensive synergism between the intraherd evaluations and the NSE and among intraherd evaluations themselves to recover the important information from the lost off-diagonals if the simultaneous approach is to be paralleled. All evaluations must incorporate any appropriate information from other evaluations.

Such synergism is actually built into a simultaneous evaluation; many problems of both technique and policy remain to be solved before it can be achieved for individual evaluations. One necessary manifestation of the required synergism has been the topic of this dissertation.

Describing a step-by-step process for implementing these procedures in industry is difficult because of the number of possible approaches. In general, a report for each recording herd would be issued twice a year using adjustments calculated from the most recent annual sire evaluation. When the initial records for an entire calf crop were received for a herd, a report would be generated covering birth and weaning traits. A second report would be issued when the yearling records were received. Possibly the sire evaluation itself would be divided into separate weaning and yearling analyses, each timed to use the greatest possible amount of recent information so that the adjustment factors would be as appropriate as possible.

On the technical side, one problem yet to be faced is the derivation of an appropriate expression for prediction error variance (PEV) that takes the variance of the herd adjustment into account. The accuracy of intraherd comparisons is, of course, unaffected by the addition of a constant factor, but the accuracy of interherd comparisons is not. One of the difficulties lies in finding an adequate approximation for PEV when an iterative solution strategy is used. Approximations such as that developed by Ufford et al. (1979) depend on the reciprocals of the diagonal coefficients being a good approximation of the inverse diagonals, which situation occurs when the diagonal coefficients are relatively large and the matrix sparse. First, this structure does not hold for equations constructed from the intraherd animal model. Second, this approximation method does not estimate sire covariances; thus, it is hard to place any confidence in the transformation of the sire variance-covariance matrix that yields estimates of the herd ad-

justment variances.

Each intraherd evaluation would be performed following receipt of a set of records that did not contribute to the sire evaluation from which the herd adjustment factor was derived. Whether or not this problem is of trivial consequence depends on the slope of the intraherd trend. Further technical study is needed to determine the magnitude of the problem and the nature of possible corrective actions.

The existence of a herd adjustment makes the incorporation of any breeding value already adjusted to the national base a simple matter. The adjustment is merely subtracted from the value to be incorporated before applying the incorporation procedures previously described. However, incorporating a value computed in a past evaluation, such as the value as a calf of a cow purchased from another herd, is no longer so simple if the national base if floating rather than fixed. Can a simple adjustment be made for the amount of float since the value was first computed? Furthermore, if an animal were purchased from a non-recording breeder, then there would be no prior value to aid in evaluating the individual properly in relation to the remainder of the herd. How should such animals be modeled?

Many other questions of methodology are also unanswered, such as those concerning the need for grouping and the need to account for inbreeding in intraherd models. To answer a number of the questions will require in-depth studies of field data to identify important features of beef population structures.

The policy decisions needed also require considerable thought. For example, a common breed association policy is to omit bulls from

national sire summaries if they fail to meet a minimum accuracy level. If a similar policy governing the performance of intraherd evaluations is desired, what is the accuracy criterion to be? Additionally, how would the association serve those herds which don't or can't meet the criterion?

Another important policy problem involves the publication method: to whom and how will the results of intraherd evaluations be made available? Should the predictors be given as estimated breeding values or as transmitting abilities? This problem has broad implications with respect to insuring the use of the latest results for each herd and maintaining breeder trust in the integrity of the program. In any format, the availability of intraherd reports will have profound effects on the marketing of breeding stock, effects that must be foreseen, anticipated, and considered in the formation of policy.

In view of the problems faced, the application of intraherd mixed-model evaluations in industry is at least 2 to 5 years away, depending mostly on the commitment of researchers to answering the technical questions. In view of the need for these programs, it is to be hoped that 5 years is also an upper limit.

SUMMARY

An adjustment factor for herd genetic merit was algebraically derived from mixed-model national sire evaluation (NSE) procedures. The adjustment was shown to be a weighted average of the NSE predictors for those sires with progeny records in the herd. This factor could be used to adjust the predictors from an intraherd mixed-model evaluation to the base of the NSE by simply adding the factor to each predictor.

The behavior of this adjustment factor was tested using simulated postweaning average daily gain records from 20 herds: 18 breeding 50 cows per year and two breeding 150 cows per year. Five cycles of breeding and calving were simulated, and sire evaluations were performed in each of the last four years of the run, producing four sets of 20 true (TA) and estimated (EA) herd adjustments. In addition, the absolute error (AE) of adjustment was calculated for each of the 80 observations as $|TA - EA|$.

The trends in AE, TA, and EA were all linear, amounting to 0.006, 0.014, and 0.024 kg/year, respectively. The increase in error over time is attributed to different trend rates in the sire and dam breeding populations.

Neither herd size nor any of five measures of the strength of the ties between herds had any significant effect on AE.

The ability of EA to properly reflect true herd differences was studied in two ways. First, the rank correlations between EA and TA were computed for each of the four sets of values. Second, the herds

within each set were randomly paired and paired-comparison t tests were performed on the average differences between the true and estimated pair differences. Both studies show that the EA from the first evaluation were poor indicators of actual herd differences and that the EA from later evaluations were acceptable.

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Out amid the cornfields,
There's an awful zoo;
God created hell on earth,
And called it ISU.

Hi, Dave.